

Ideal free distribution of fixed dispersal phenotypes in a wing dimorphic beetle in heterogeneous landscapes

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Abstract. According to the ideal free distribution (IFD) theory, individuals that are able to perceive the quality of different patches in a landscape and disperse freely are expected to redistribute themselves proportionally to the carrying capacities of heterogeneous patches. Here, we argue that, when dispersal is unconditional and genetically fixed, a coalition of sedentary and dispersing phenotypes can attain an IFD under spatiotemporally uncorrelated variation in fitness. This not only leads to a stable polymorphism of both dispersal phenotypes, but also implies that the number of dispersing individuals should on average be equal among patches and determined by the carrying capacity of the smallest local populations in the landscape. Differences in carrying capacity among patches are thus only reflected by changes in the number of sedentary individuals. Individual-based simulations show that this mechanism can be generalized over a wide range of spatiotemporal conditions and dispersal strategies. Moreover, these expectations are in strong agreement with empirical data on the density of both dispersal phenotypes of the wing dimorphic ground beetle *Pterostichus vernalis* within and among 10 different landscapes. Hence, for the first time, these results demonstrate that this mechanism serves as a plausible alternative to the competition-colonization model to explain the spatial distribution of fixed dispersal phenotypes in heterogeneous landscapes. Understanding of the frequency distributions of individuals expressing discrete dispersal morphs moreover improves our predictive and management capabilities for a broad range of species, for which we currently typically rely on using mean dispersal rates.

Key words: carabid beetle; density dependence; dispersal evolution; dispersal polymorphism; ideal free distribution.

INTRODUCTION

If dispersal rates evolve such that individual fitness is optimized over the different patches in the landscape, patch-specific dispersal rates are expected to be in accordance with predictions of the Ideal Free Distribution concept (IFD; Fretwell and Lucas 1970; see also McPeck and Holt 1992, Lemel et al. 1997a, Holt and Barfield 2001, Clobert et al. 2008, Cantrell et al. 2012). As originally defined, this states that within a series of patches with positive intrinsic growth rates (i.e., sources), populated by individuals exhibiting *ideal free* behavior (i.e., that are able to move freely among patches and have complete knowledge of their environment) the fraction of individuals dispersing to a particular patch is proportional to the carrying capacity of that patch (Fretwell and Lucas 1970, Holt and Barfield 2001, Cantrell et al. 2012). It has therefore primarily been applied in both theoretical and empirical research to explain patch specific dispersal rates for

conditional dispersal behaviors (McPeck and Holt 1992, Doncaster et al. 1997, Holt and Barfield 2001, Clobert et al. 2008; but see Lemel et al. [1997b], Holt and Barfield [2001], and Cressman and Krivan [2006], wherein these assumptions are relaxed).

However, only a few attempts have been made so far to test whether predictions emerging from IFD theory can also be applied to explain the distribution of unconditional and genetically fixed dispersal phenotypes (McPeck and Holt 1992, Kirkland et al. 2006, Cantrell et al. 2012). Phenotypic constraints, such as for example strong differences in wing size in dispersal dimorphic species, render it unlikely that individuals can make optimal dispersal decisions with respect to spatiotemporal fluctuations in fitness. Recently, Cantrell et al. (2012) showed that a coalition of populations that only differ in their dispersal strategy can distribute themselves such that they exactly match the distribution of resources in the landscape, and as such function as a population using an ideal free dispersal strategy. At present, none of these theoretical studies tested the validity of these results under more realistic settings such as stochastic fluctuations in patch quality. This is crucial as Schreiber

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(2012) demonstrated that these environmental settings may disrupt the classical IFD predictions.

More important, there are at present no empirical studies that attempt to test if variation in fixed dispersal phenotypes is indeed in accordance with the predictions of IFD theory. Although numerous studies compared empirical data with clear theoretical expectations (e.g., Roff 1994, Doncaster et al. 1997, Heino and Hanski 2001, Hanski et al. 2004, Baguette et al. 2011), the main focus has been on the evolution of mean emigration rates in relation to various patch and landscape characteristics, rather than comparing the densities of discrete dispersal phenotypes among patches within an IFD framework. Empirical work on the distribution of fixed dispersal phenotypes has currently also only been interpreted within the context of extinction–colonization dynamics, wherein the dispersing morph is able to colonize vacant patches and becomes replaced at later stages by the sedentary morph due to the latter's presumed superior competitive ability (Roff 1986, Denno et al. 1996, 2001, Dhuyvetter et al. 2007, Roff and Fairbairn 2007).

Here, we argue that in line with the IFD theory, some general predictions can be deduced concerning the distribution of individuals with a dispersing and sedentary phenotype in spatiotemporally variable landscapes. A general outcome of theoretical work on dispersal evolution is that dispersal is generally favored under spatially and temporally uncorrelated variation in fitness among patches (Hastings 1983). Under the assumptions that all the individuals disperse unconditionally and immigrate at random irrespective of the patch quality (i.e., they are non-ideal) this will lead to overpopulation, and thus lower individual fitness, in low quality patches and higher individual fitness in high quality patches. This results in source–sink dynamics, wherein individuals on average disperse from high quality to low quality patches, and landscapes with spatial variation in habitat quality are therefore expected not to favor a dispersal strategy (Hastings 1983, Holt 1985). However, as random dispersal will lead to an equal number of dispersers in all patches, overpopulation in low quality habitat will not occur if the number of dispersing individuals in each patch does not exceed the carrying capacity of the lowest quality patches in the landscape. Higher quality patches on the other hand will be strongly underpopulated and the remaining individuals inhabiting these patches will consist principally of the sedentary phenotype.

In summary, we predict for unconditional and fixed dispersal strategies that (1) the number of individuals of the dispersing phenotype should approximate a random distribution among patches, (2) the number of dispersing individuals in each patch is independent of patch capacity and approaches the carrying capacity of the most inferior patches present in the landscape, and (3) the number of sedentary individuals in each patch will in contrast depend strongly on the local patch capacity.

Consequently, the proportion of individuals of the dispersing phenotype should be strongly negatively correlated with population size.

We compare these predicted distributions with those observed from both stochastic individual-based simulations performed under a wide range of spatial and temporal conditions and dispersal strategies as well as on the observed distribution of the number of both short- (brachypterous) and long-winged (macropterous) individuals of the wing dimorphic ground beetle *Pterostichus vernalis* within and among 10 different landscapes.

MATERIAL AND METHODS

Individual-based model description

The landscape structure comprised 20×20 patches on a square lattice. Spatial heterogeneity was introduced by assigning patch-specific mean carrying capacities, \bar{K}_i , sampled from a normal distribution with landscape mean, \bar{K} , and a spatially uncorrelated variance, σ_{sp}^2 . A lower bound for \bar{K}_i in the landscape, further denoted as K_{min} , was specified to compare the effect of minimum patch carrying capacity on demographic parameters and reflects a minimum patch quality before individuals will settle. Hence, patch specific carrying capacities were distributed according to $\bar{K}_i = \max\{N(\bar{K}, \sigma_{sp}^2), K_{min}\}$. Temporal variation in patch carrying capacities was implemented at each yearly time step, to which the K_{min} lower bound was again applied, by sampling from the distribution $K_i(t) = \max\{N(\bar{K}_i, \sigma_{temp}^2), K_{min}\}$.

We considered an asexual species consisting of dispersing and sedentary individuals as well as a sexual species where the dispersal phenotype is determined by a two-allele mechanism, with the sedentary allele being dominant (equivalent to the genetic determination of macropterous and brachypterous individuals in our empirical system, see *Empirical model system: Density of dispersing and sedentary individuals in relation to population size in real landscapes*). Only dispersing individuals were able to colonize other patches in the landscape and sedentary individuals always stay in their natal patch.

We implemented three different dispersal methods. First, dispersers dispersed globally and all patches were equally likely to receive immigrants. In the second case, dispersal distance was restricted and dispersers were only able to colonize neighboring patches. Third, dispersal was conditional on the patch density,

$$D_i(t) = \frac{K_i(t) - N_i(t)}{K_i(t)}$$

such that underpopulated patches were more likely to receive immigrants. Here, a dispersing individual chose a patch at random in the landscape with probability

$$P = \exp[D_i(t)] / (1 + \exp[D_i(t)]).$$

For the asexual species, dispersal was followed by reproduction and population regulation. For the sexual

species, the series of events was modeled according to the life history of the study species *Pterostichus vernalis* (see *Empirical model system: Density of dispersing and sedentary individuals in relation to population size in real landscapes*), i.e., individuals first mate with each other in their natal patch, disperse afterward and reproduce once settled in a particular patch.

Regulation of population densities followed the Beverton-Holt model where each of $N_i(t)$ adults within a patch produces λ offspring, which we allowed to be different for sedentary and dispersing individuals, that compete with each other leading to patch specific population sizes equal to

$$N_i(t+1) = \lambda N_i(t) / [1 + a_i(t) N_i(t)]$$

with parameter $a_i(t) = [(\lambda - 1)/K_i(t)]$.

After population regulation, the number of dispersing and sedentary individuals was recorded each generation, and these individuals made up the next generation that respectively underwent dispersal, reproduction and population regulation.

The cost of dispersal was implemented as the probability of mortality during the dispersal phase, m . Whereas under sexual conditions brachypterous individuals and alleles can be introduced to local populations through eggs produced by immigrant females that were mated in patches with brachypterous males, that was not possible in the asexual model. Therefore, to allow the introduction of sedentary individuals after stochastic extinction in a patch in the model, we implemented a small reciprocal probability of mutation between sedentary and dispersing genotypes in the asexual model only. Annotated computer code used to perform the simulations can be found in Supplement 1.

In a first series of our simulation experiments, we investigated how the dispersal method affects the dynamics and absolute numbers of both dispersal phenotypes within local populations. This was performed under the following population and landscape parameters: $\bar{K} = 50$, $\sigma_{sp} = 50$, $\sigma_{temp} = 5$ and a minimal carrying capacity at which we assumed a local population can persist or settle, i.e., K_{min} , equal to 20 individuals. To obtain the average frequencies of both dispersal phenotypes per patch, further denoted as N_{Si}^* and N_{Di}^* for sedentary individuals and dispersers respectively, we first visually inspected the dynamics and selected the last 500 generations for which no monotonic increase or decrease in the proportion of dispersing individuals was present. This was further confirmed by the absence of a significant relationship between the total proportion of dispersing individuals in the landscape and generation number. N_{Si}^* and N_{Di}^* were then obtained by averaging $N_{Si}(t)$ and $N_{Di}(t)$ for these last 500 generations. In addition, we inspected the distribution of both phenotypes within a single generation in order to compare the simulated data with the empirical data, which also originate from a single generation sampling. For these single generation data,

we investigated the extent to which the variance in frequency of dispersers in each patch differs from a random Poisson expectation by calculating the Pearson χ^2 overdispersion parameter (ϕ). Next, we investigated how variation in σ_{sp} , σ_{temp} , K_{min} , m , and a dispersal-related fecundity trade-off affects the equilibrium numbers of both dispersal phenotypes in each local population.

Empirical model system: Density of dispersing and sedentary individuals in relation to population size in real landscapes

Study organism.—Intraspecific variation in dispersal ability was assessed in the ground beetle *Pterostichus vernalis*. It has a Palaearctic distribution and is fairly common in natural as well as agricultural habitats throughout its geographic distribution. It is preferentially found in rather moist eutrophic grasslands and to a lesser extent in eutrophic marshes. Flight records, as assessed by window traps and field observations, demonstrate that the species is capable of long-distance dispersal (Greenslade and Southwood 1962, Van Huizen 1980, Desender 1989). The distribution of wing length follows a clear bimodal distribution with short-winged (brachypterous) and long-winged (macropterous) individuals (Turin 2000; F. Hendrickx, *personal observation*). As flight records always involve macropterous individuals, and brachypterous individuals lack functional flight musculature, this indicates that only the macropterous form is able to perform movement by flight (Desender 1989). Information about the genetic basis of wing size is not yet available for this particular ground beetle species. However, all studies on the genetic basis of wing dimorphism in ground beetles, including the related species *Pterostichus anthracinus*, indicate that the trait is genetically based and follows an inheritance pattern as expected from a single locus with two alleles with brachypterous dominant over macropterous (Lindroth 1946, Roff 1986, Desender 1989). Dispersal in carabid beetles takes place primarily after mating but before egg laying. Once settled, flight muscles undergo autolysis into adipose tissue that is used for egg production (Turin 2000).

Sampling design.—Individuals were captured in 10 different agricultural landscapes distributed over three different temperate European countries: Belgium (four landscapes), Switzerland (two landscapes), and the Netherlands (four landscapes). Most carabid beetles, including the study species *Pterostichus vernalis*, are epigeic and occur typically at low densities, rendering it impossible to obtain a complete picture of their distribution in a landscape. Rather than sampling distinct patches, sampling was conducted such that both the species distribution within the landscape as well as a relative estimate of the local and landscape population density could be obtained. The rationale behind our sampling strategy was that, within each landscape, traps were installed at approximately equally spaced distances

within the dispersal distance of long-winged individuals, but beyond that of short-winged individuals within a single generation. Based on a large capture–recapture study on the related and strictly brachypterous species *Pterostichus lepidus*, only short distances of 50–150 m are reached within a single generation in suitable habitat, while unsuitable habitat is strictly avoided (Vermeulen 1994). Long-winged individuals of carabid beetles of similar size are in contrast able to disperse distances that span several kilometers, as evidenced from colonization of macropterous carabid species in recently created habitat separated by such distance from the nearest source population (den Boer 1968) and aerial migration at heights between 175 m and 246 m above ground level of macropterous individuals of the wing-dimorphic species *Notiophilus biguttatus* (Chapman et al. 2005). Based on these studies, we assumed that distances of approximately 1 km are within dispersal distance of long-winged, but not of short-winged individuals and that spatiotemporal uncorrelated variation in fitness at distances of 1 km cannot be compensated by dispersal of short-winged individuals.

Each landscape measured 4 km \times 4 km and was divided into 16 subplots of 1 km². To estimate the relative population densities, each subplot was sampled with a trap set consisting of two pitfall traps (diameter 10 cm, filled with 4% formaldehyde solution and some detergent) placed between 25 m and 50 m apart. They were placed at the border of a randomly chosen seminatural habitat patch (field margins, hedgerows, seminatural grasslands, set aside fields and forest) and an agricultural field. Traps were active for 7 weeks in spring and 5 weeks in autumn. As traps were placed at random without taking habitat preference of the species into account, this sampling design allows data to be obtained from both favorable (i.e., reflecting high K), as well as less suitable (i.e., low K) habitats in the landscape. As a measure of habitat suitability, the percentage of coverage of its preferred habitat, i.e., moist eutrophic grassland, was estimated in a radius of 50 m around each trap. This distance has proven to be useful to relate habitat environmental data to carabid assemblages (Hendrickx et al. 2009) and has been shown to be an average walking distance within a single generation of short-winged individuals of the related species *Pterostichus lepidus* (Vermeulen 1994).

Elytra length and wing size of all individuals were measured to the nearest 0.05 mm. To determine the dispersal ability of each individual, wing length was regressed against elytra length. The residual wing lengths clearly revealed a bimodal distribution and each individual could unequivocally be assigned as brachy- or macropterous.

Statistical analysis.—To test for the relationship between proportion of macropterous vs. total number of individuals in a trap set, a mixed model logistic regression was performed with total number of captured individuals per trap set as fixed independent variable

and landscape as a random effect (Proc glimmix in SAS 9.3 [SAS Institute 2011]).

To verify if the total number of captured individuals in a trap set indeed reflects differences in the carrying capacity in terms of habitat suitability, totals were regressed against the proportion of wet eutrophic grassland cover around the traps by means of an overdispersed Poisson regression, and its significance was assessed by means of a Type III likelihood ratio test (Proc genmod, SAS 9.3).

Variation in density of macropterous and brachypterous individuals among local populations (i.e., trap sets) was quantified by means of the Pearson χ^2 overdispersion parameter, ϕ . This statistic corresponds to the ratio of the observed variance in numbers to the expected variance under a Poisson distribution and is as such independent of the mean abundance. This statistic was obtained by fitting a logistic generalized linear model with landscape as an independent variable (Proc genmod, SAS 9.3). To test if the degree of overdispersion is larger than 1, indicating that the variance in frequencies among trap sets within a landscape is larger than expected from a random distribution, the observed value was not tested against a χ^2 distribution as the average number of captured individuals was too low to fulfill the assumptions of this large sample test (Agresti 2002). We therefore obtained the null distribution of the overdispersion parameter based on a parametric bootstrap. Differences in the number of captured brachy- and macropterous individuals among landscapes were tested by means of logistic regression, again with landscape as an independent categorical variable.

RESULTS

Individual-based simulation

Considering an asexual species, global dispersal, and the absence of dispersal mortality, the average number of individuals in each patch with the sedentary phenotype, N_{Si}^* , correlated almost perfectly with the mean carrying capacity of the patch (Fig. 1a). Only for the smallest patches in the landscape ($K_i \leq 40$ in Fig. 1a), the number of sedentary individuals per patch decreased abruptly, indicating that the sedentary phenotype does not persist in these smaller patches. The number of individuals with the dispersing phenotype in each patch, N_{Di}^* , appeared independent of the local patch capacity and was approximately equal among all patches in the landscape. The average number of N_{Di}^* , 23.97, closely approximated the predicted value of $K_{\min} = 20$. These results were robust to dispersal method, including dispersal restricted to neighboring patches (Fig. 1b) and even global dispersal with immigration proportional to $N_i(t)/K_i(t)$ (Fig. 1c), for which N_{Di}^* was equal to 23.90 and 23.46, respectively.

For the sexual species, a similar pattern was observed with an even tighter relationship between patch capacity

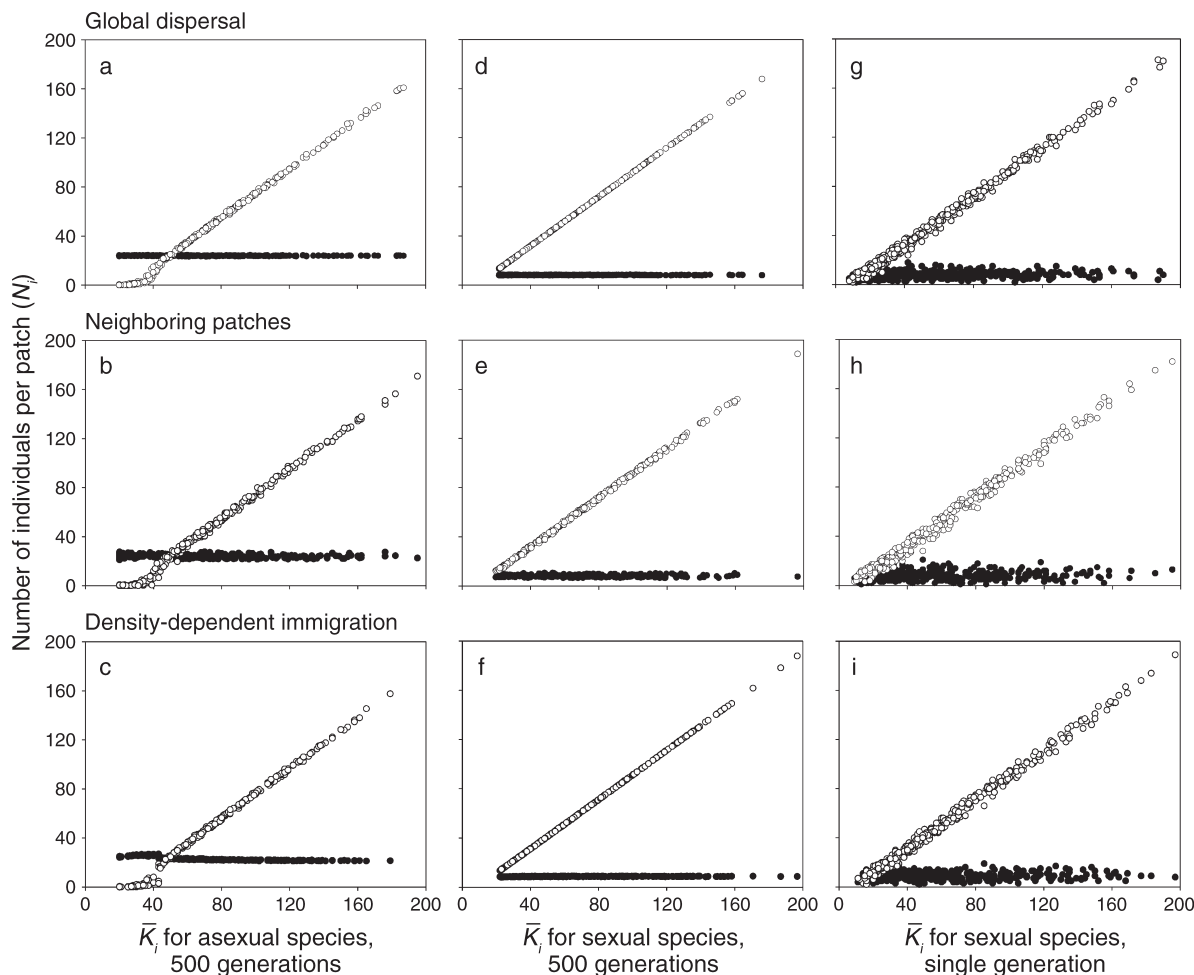


FIG. 1. The number of individuals with sedentary (open circles) and dispersing (solid circles) phenotype (N_i) in relation to mean patch carrying capacity (\bar{K}_i). These results are from a simulation of a landscape that consisted of 400 patches under a scenario of (a, d, g) global dispersal of individuals across the landscape, (b, e, h) dispersal of individuals that is restricted to neighboring patches, and (c, f, i) global dispersal of individuals with immigration probability dependent on the patch carrying capacity. Values represent the average of the last 500 generations out of 1000 generations from both (a–c) an asexual and (d–e) a sexual species. Panels (g)–(i) depict the results of the last generation only for a sexual species. Patch and landscape parameters were: average patch capacity, $\bar{K} = 50$; minimum patch capacity, $K_{\min} = 20$; spatial variation in \bar{K}_i , $\sigma_{sp} = 50$; temporal variation in $K_i(t)$, $\sigma_{temp} = 5$.

and the number of sedentary individuals per patch and a homogeneous distribution of dispersing individuals across patches (Fig. 1d). As for the asexual species, the results were highly consistent for the different implemented dispersal methods (Fig. 1d–f). However, compared to the asexual case, the number of dispersers in each patch was considerably lower than the minimum patch capacity, with N_{Di}^* being equal to 8.25, 8.24, and 8.70 under global, neighboring, and density-dependent immigration, respectively. Within a single generation the number of dispersers within a patch was more variable, and larger than expected from a random Poisson distribution for all dispersal methods ($\phi_{NDi} = 3.12$, $\phi_{NDi} = 3.25$, and $\phi_{NDi} = 2.70$ under global, neighboring, and density-dependent immigration, respectively; Fig. 1g–i).

To further investigate the dependency of N_{Di}^* to K_{\min} , simulations were first performed with an asexual species

with global dispersal, but we varied the minimum patch capacity in the landscape from $K_{\min} = 0$, which represents the presence of deterministic sink patches in the landscape, to $K_{\min} = 60$. Within each local population, the average number of dispersers in each patch corresponded almost perfectly with the lowest patch capacity present in the landscape (Fig. 2a, solid circles). This pattern remained unaffected for simulations with different values of temporal variation (e.g., $\sigma_{temp} = 20$; Fig. 2a, solid triangles). Also, changing spatial variation did not affect the strong dependency of N_{Di}^* to K_{\min} , but resulted in a slightly higher number of dispersers in each patch, in particular for lower values of K_{\min} (e.g., $\sigma_{sp} = 50$; Fig. 2a, open circles). These simulations further demonstrated that individuals with the dispersing phenotype persist when sinks are present in the landscape.

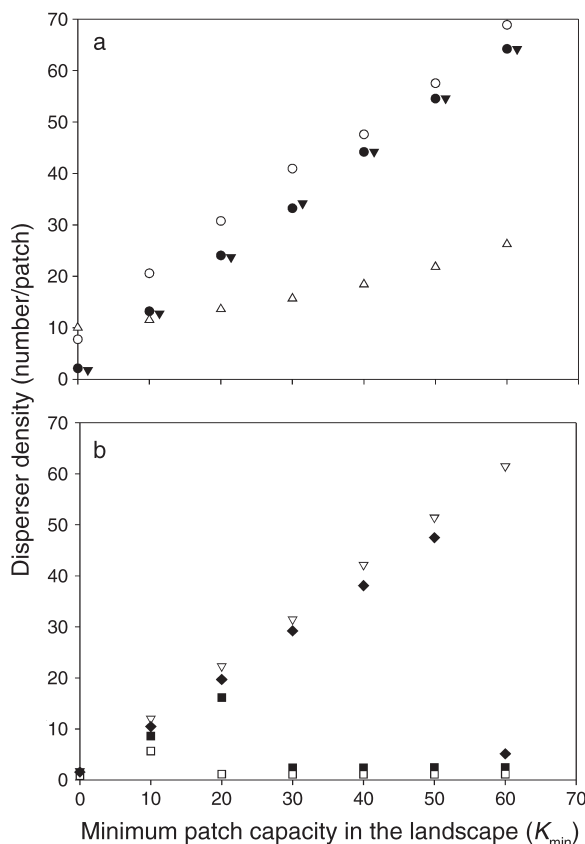


FIG. 2. The average number of dispersing individuals in each patch in relation to the size of the smallest patches in the landscape (K_{\min}). (a) Mean patch capacity, $\bar{K} = 100$, and dispersal mortality, $m = 0$; asexual individuals and $\sigma_{\text{sp}} = 100$ and $\sigma_{\text{temp}} = 5$ (solid circles); asexual individuals and $\sigma_{\text{sp}} = 50$ and $\sigma_{\text{temp}} = 5$ (open circles); asexual individuals and $\sigma_{\text{sp}} = 100$ and $\sigma_{\text{temp}} = 20$ (solid triangles); sexual diploid individuals and $\sigma_{\text{sp}} = 50$ and $\sigma_{\text{temp}} = 5$ (open triangles). (b) Mean patch capacity, $\bar{K} = 100$, $\sigma_{\text{temp}} = 5$, $\sigma_{\text{sp}} = 100$, asexual individuals and dispersal mortality values, m , of 0.01 (open triangles), 0.025 (solid diamonds), 0.05 (solid squares), and 0.1 (open squares). Values represent the average of the last 500 generations out of 1000 generations.

Although this pattern remained unchanged when a low dispersal mortality was assumed ($m = 0.01$; Fig. 2b), strong deviations from this global pattern were observed under higher levels of dispersal mortality. Here, the dispersal strategy was no longer favored due to the high dispersal costs, but this effect only occurred when the minimal patch capacity in the landscape was large.

Considering a sexual species and global dispersal, the strong relationship between minimum patch capacity and number of dispersers per patch persisted, albeit that this number was substantially higher than expected when sinks are present in the landscape (i.e., $K_{\min} = 0$) and lower than expected for higher values of K_{\min} (Fig. 2a, open triangles). All else being equal, incorporating a dispersal related fecundity trade-off, which was implemented by changing λ of the dispersing phenotype while

keeping $\lambda = 3$ for the sedentary phenotype did not appear to affect the number of sedentary individuals per patch ($N_{\text{Di}}^* = 8.32, 8.72$, and 8.62 for $\lambda_{\text{disp}} = 2.5, 2.0$, and 1.5 , respectively).

Empirical model system: Density of dispersing and sedentary individuals in relation to population size in real landscapes

A first prediction that emerges from this theory is that variation in the frequency of macropterous individuals among the different patches within a given landscape is low and primarily due to stochastic variation. For brachypterous individuals, in contrast, it is expected that the variation in number among patches is more variable and relates to the size of the local populations.

In accordance with these predictions, the variance of the number of captured macropterous individuals among trap sets within a landscape was only about twice as high as expected under a random distribution ($\phi_{\text{mac}} = 2.17$; bootstrap $P < 0.0001$), while the variance in the number of captured brachypterous individuals was substantially larger and more than nine times higher than expected under a Poisson distribution ($\phi_{\text{brac}} = 9.43$; bootstrap $P < 0.0001$).

Differences in the total number of captured individuals per trap set was significantly and positively related to the amount of suitable habitat both when assessed across all sampled sites (slope = 0.0038, SE = 0.0012, $F_{1,157} = 6.67$, $P = 0.008$) as well as within landscapes (slope = 0.0016, SE = 0.0008, $F_{1,148} = 5.28$, $P = 0.02$). Although both the number of brachypterous and macropterous individuals captured per trap set was significantly correlated with the total number of individuals captured in each trap set ($P < 0.01$), the strength of this correlation was much stronger and almost perfectly linear for the brachypterous individuals ($r = 0.99$) compared to the macropterous individuals ($r = 0.27$; Fig. 3a and b). As a consequence, the proportion of macropterous individuals in each local population was negatively correlated with local population size (logit(Pr_{mac}) vs. N_{tot} ; slope = -0.051 ; SE = 0.0122; $F_{1,94} = 18.00$, $P < 0.0001$; Fig. 3c).

Moreover, the number of captured individuals per trap set averaged across the landscape did not differ between landscapes for macropterous individuals ($F_{9,91} = 0.76$, $P = 0.7$), but was highly different for brachypterous individuals ($F_{9,91} = 7.84$, $P < 0.0001$; Fig. 4). Consequently, the proportion of macropterous individuals was strongly negatively correlated with the total number of individuals captured in the landscape ($r_s = -0.8$, $P = 0.005$).

DISCUSSION

When individuals of a species with a fixed dispersal dimorphism redistribute themselves in a heterogeneous landscape with spatially uncorrelated environmental variation, we expected the frequency of dispersers to be equal among patches, while the frequency of

sedentary individuals should be strongly related to the carrying capacity of the patch. Consequently, the proportion of dispersers in local populations should decrease monotonically with respect to local population density.

*Distribution of fixed dispersal phenotypes:
individual-based simulations*

Results of our numerical simulations are congruent with these observations, and moreover showed that this result holds under a wide variety of dispersal types. Hence, irrespective of whether dispersal is global, restricted to neighboring patches, or dependent on local population size, a similar outcome was observed. Moreover, these simulations demonstrated that the frequency of dispersing individuals in each patch is strongly determined by the carrying capacities of the smallest habitat patches in the landscape. Indeed, if all individuals in the landscape emigrate and dispersal is random over all patches, the number of individuals colonizing the smallest patches in the landscape will on average be substantially larger than their carrying capacities. Under this condition, the dispersal strategy will be selected against until the number of dispersing individuals in each patch approaches the carrying capacity of the smallest patches and random dispersal will in this case not lead to overpopulation in inferior patches.

However, results of our simulations also show some subtle, though important deviations from these classical IFD predictions. First, the number of dispersers in each patch is slightly but consistently higher than the specified minimum patch capacity (Fig. 2a). Consequently, and contrary to deterministic IFD predictions, the dispersal phenotype does not go extinct when sinks are present in the landscape. These results are consistent with those of Schreiber (2012), who recently showed that high levels of spatially uncorrelated environmental stochasticity still favor the selection of deterministic sink patches resulting in overmatching of low quality patches. Within the context of a coalition of a low and high unconditional dispersal strategy, this is equivalent to the persistence of high dispersers in the landscape and their occupation of sink patches. Second, for the asexual model, the number of sedentary individuals does not decrease linearly with decreasing patch capacity for patches that approach K_{\min} (e.g., patches with $K_i \leq 40$ in Fig. 1). This is likely due to the fact that for patches with low carrying capacities, competition between sedentary and dispersing individuals may cause stochastic extinctions of the former. In other words, for sedentary individuals, low quality patches may act as stochastic sinks, i.e., they exhibit negative local stochastic growth rates but positive intrinsic growth rates (Schreiber 2012). Indeed, Schreiber (2010) showed that under the assumption that both dispersal types persist at stationarity in landscapes with spatiotemporal uncorrelated fluctuation, not all patches can be occupied by

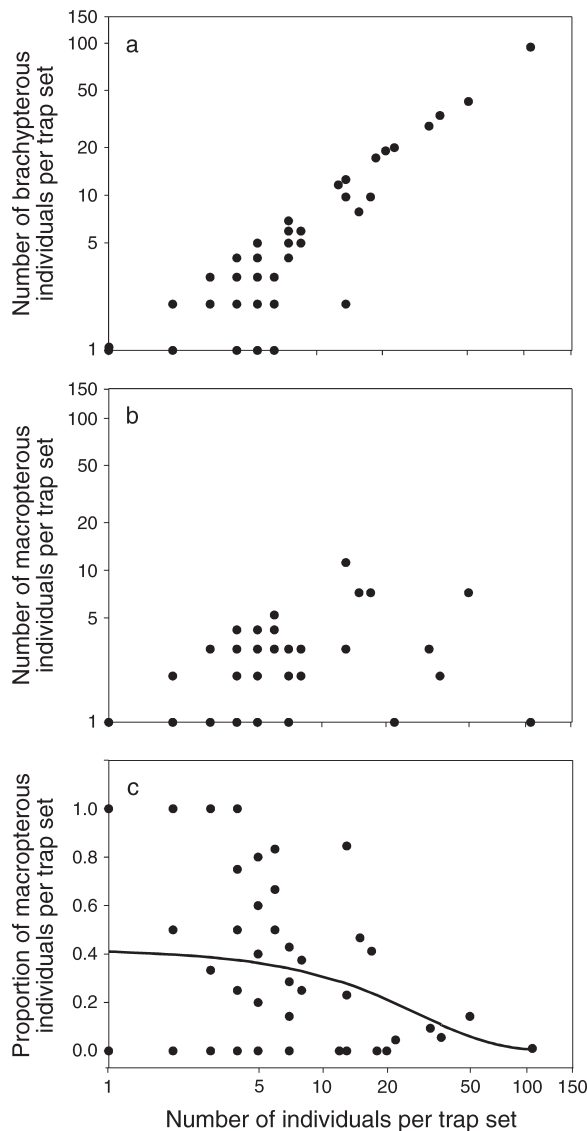


FIG. 3. Number of (a) brachypterous and (b) macropterous individuals and (c) the proportion of macropterous individuals in relation to the total number of individuals of *Pterostichus vernalis* captured in a trap set consisting of two pitfall traps.

sedentary individuals. This follows from the fact that, at stationarity, both local growth rates of non-dispersers and spatially averaged growth rates of dispersers are zero. This results in negative growth rates in patches without sedentary individuals, which can only be occupied by dispersers. Third, the extinction of sedentary individuals in these smaller patches was not observed when we modeled a sexual species. This can be attributed to the sequence of life history events that we implemented. As individuals mate in their natal patch, but reproduce after the dispersal event, local extinction of sedentary individuals is prevented by the repeated production of sedentary offspring by dispersing individuals. This mechanism also explains the substan-

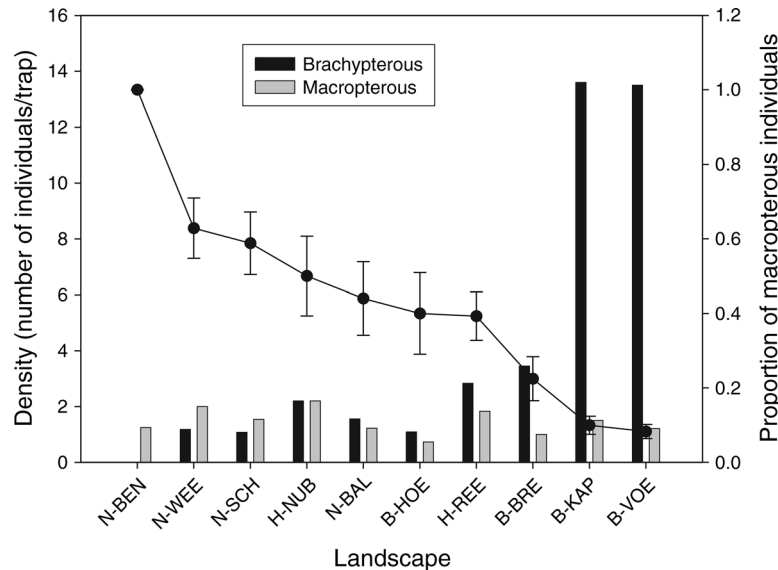


FIG. 4. Average number of captured macropterous (gray bars) and brachypterous (black bars) individuals per trap set in 10 different landscapes ($4 \text{ km} \times 4 \text{ km}$) distributed over Europe (N, The Netherlands; H, Switzerland; B, Belgium). Line-connected dots represent the average proportion of macropterous individuals in each landscape (right-hand y-axis). Error bars depict standard errors.

tially lower number of dispersers in each patch compared to the asexual model.

Distribution of fixed dispersal phenotypes: empirical data

Subsuming long and short winged individuals in *Pterostichus vernalis* as dispersing and sedentary individuals, results from our empirical system are in strong agreement with these IFD predictions, with a significantly lower proportion of long-winged individuals observed in high density populations. To verify if this negative relationship can be attributed to the homogeneous distribution of dispersers throughout the landscape, we compared the variation in their frequency with those expected from a Poisson distribution. This revealed that the distribution of dispersers matches such a random distribution much more closely compared to variation in the number of sedentary individuals. The somewhat higher variance in number of dispersers than expected under a Poisson distribution can be attributed to several issues. First, the data at hand originate from a single season sampling campaign and stochastic variation in population numbers due to both extrinsic and intrinsic factors as well as sampling variation might result in a slight deviation from a random distribution of macropterous individuals. Second, the genetic system that determines wing size might result in a slower response in the distribution of dispersal types than expected under a mere ecological model (Roff 1994, Denno et al. 1996, 2001, Roff and Fairbairn 2007). This was confirmed by our simulations of the sexual species showing that even under global dispersal the variance in the frequency of dispersing individuals is about three times larger compared to the expected variance under

Poisson expectations and agreed reasonably well with the variance observed for our empirical data. These factors are however unlikely to cause the observed differences in the total number of brachypterous individuals in each local population as this would result in an equal degree of overdispersion in the numbers of both dispersal types among patches. Hence, the more than four times higher degree of overdispersion in number of brachypterous individuals among populations strongly suggests that this primarily reflects variation in carrying capacity among populations. This was further confirmed by the positive relationship between habitat suitability and the total number of captured individuals within each trap set.

The mechanism that determines the number of dispersing individuals in each patch and, hence, the minimum patch capacity, is unfortunately hard to test directly in natural populations. First, a minimum patch capacity that is larger than zero is most likely determined by a minimal degree of habitat suitability before dispersing individuals settle (i.e., source habitats), although life history traits (Legendre 2004) or Allee effects (Stephens and Sutherland 1999) might have additional influence. As the conditions that determine this smallest local population size are in this case an intrinsic property of the species (Colas et al. 2004), they are not expected to differ substantially among landscapes. In line with this, the average number of macropterous individuals captured in each trap appeared to be remarkably similar among landscapes. This contrasted strongly with the number of brachypterous individuals, for which the average capture densities at each trap set varied from zero in landscape N-Ben to

almost 14 in landscapes B-Kap and B-Voe. Second, if the species would not be able to discriminate between source and sink habitats, resulting in frequent settlement of dispersers in sink habitats, the factors that determine the number of dispersing individuals are more complex and determined by the magnitude of temporal and spatial autocorrelation in local population fluctuations (Schreiber 2010). In turn, such fluctuations are properties of the individual landscapes, and therefore less likely to result in an equal number of dispersing individuals per trap in each landscape.

The analogy between IFD and the evolution of dispersal has primarily been introduced to explain the evolution of conditional dispersal strategies (Lemel et al. 1997a, Holt and Barfield 2001, Clobert et al. 2008). As originally defined, it is assumed that individuals are able to perceive the negative density-dependent effects caused by immigration. Such conditional dispersal strategies are predicted from theoretical studies (Travis and Dytham 1999, Poethke and Hovestadt 2001, Kum and Scheuring 2006, Bocedi et al. 2012) and confirmed by a wealth of empirical observations (Doncaster et al. 1997, Bowler and Benton 2005, Clobert et al. 2009). Here, we show in agreement with other studies (McPeck and Holt 1992, Lemel et al. 1997a, Holt and Barfield 2001, Cressman and Krivan 2006, Massol et al. 2011) that this strong “ideal” assumption is not a necessary condition for a population to attain an IFD (McPeck and Holt 1992, Lemel et al. 1997a, Holt and Barfield 2001). However, until now no empirical data were available to support these theories.

Expected distribution of fixed dispersal phenotypes under the IFD vs. the competition–colonization model

Although empirical data on wing polymorphic species played a historic and pivotal role in developing some key principles of dispersal evolution theory and in explaining dispersal polymorphisms (cf. den Boer 1968, Roff 1986), they were until now only interpreted in the context of differences in habitat persistence and local extinction of patches. In particular, the theoretical arguments and models developed by den Boer (1968) and Roff (1994) proved to be highly valuable in explaining the relative increase of long-winged individuals in recently colonized habitats (den Boer 1968, Denno 1994, Denno et al. 1996). Alternatively, the adaptive value of the wingless morph in persistent habitat patches is primarily attributed to an expected higher fecundity or earlier maturation achieved due to a lack of investment in wing muscles and other dispersal-related traits (Aukema 1991, Zera and Denno 1997, Roff and Fairbairn 2007). Under the present model and those developed by (McPeck and Holt 1992, Doebeli and Ruxton 1997), the higher fecundity of the sedentary morph is not a necessary condition to explain the coexistence of both morphs. Selection for short-winged individuals rather stems from the unconditional dispersal rate of long-winged individ-

uals, which is selected against when source–sink dynamics are reached.

If habitat persistence, rather than the density-dependent fluctuations proposed here, would be the sole factor explaining the dispersal polymorphism in *P. vernalis* the number of dispersers per patch would be expected to be dependent on the local population size and a much larger degree of overdispersion in the number of dispersers among patches and landscapes would be expected. To confirm this we adapted the model previously developed by Roff (1994) allowing for spatial variation in K_i and investigated the relationship between the number of brachy- and macropterous individuals and patch capacity. This indeed shows that under patch extinction dynamics (i) the frequency of dispersers increases strongly with increasing patch capacity and (ii) that the variance in the number of long-winged individuals is much larger than expected from a random distribution (see the Appendix and Supplement 2 for the results of the simulation and the code). It nevertheless remains very reasonable that if local extinctions occur in the landscape, they will first be occupied by long-winged individuals that will decrease in proportion after the colonization event. However, our data suggest that local extinctions and dispersal related fitness trade-offs (cf. Roff 1986, Haag et al. 2005, Roff and Fairbairn 2007) are not a necessary prerequisite to explain the evolution and persistence of dispersal dimorphisms.

Frequency of dispersal phenotypes vs. dispersal rates

Another important conclusion that arises from this work is that concentrating solely on the average dispersal rate, or the proportion of both dispersal polymorphisms, may lead to spurious conclusions concerning a population's colonization ability in response to habitat deterioration. An increase in the proportion of macropterous individuals due to decreasing local population sizes, and consequently increased local extinction rates (Hanski 1998), could be interpreted as an evolutionary “rescue effect” against metapopulation extinction (Heino and Hanski 2001, Parvinen 2004). In this study, an increase in the proportion of macropterous individuals in response to these factors is only determined by a decrease in the number of brachypterous individuals. As the number of macropterous individuals in the landscape is much less affected, colonization ability within the landscape remains unaltered despite the observed increase in average dispersal rate.

Besides the fact that this is to our knowledge the first empirical verification of the distribution of a dispersal polymorphism within an IFD framework, our results further emphasize that interpretation of the frequency of individuals expressing discrete dispersal morphs in a landscape, rather than simply mean dispersal rates, could greatly enhance our understanding of the mechanisms that underlie interdemographic variation in dispersal rates and such consideration is therefore required in

future empirical and theoretical studies of dispersal evolution and in conservation research.

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SUPPLEMENTAL MATERIAL

Appendix

Expected distribution of fixed dispersal phenotypes under the competition–colonization model described in Roff (1994) ([Ecological Archives E094-228-A1](#)).

Supplement 1

C++ source code to model the spatial distribution of fixed dispersal phenotypes as described in this paper and a short description of the program and its options ([Ecological Archives E094-228-S1](#)).

Supplement 2

R code to model the spatial distribution of fixed dispersal phenotypes under competition–colonization dynamics as described in Roff (1994), but allowing for spatial variation in K ([Ecological Archives E094-228-S2](#)).